THE HOMOLOGIES OF THE UREDINEAE (THE RUSTS).

By Charles E. Bessey.

The place of the parasitic plants constituting the Order *Uredineae* (The Rusts), in a natural system of classification, has long been in doubt, botanists not being fully agreed as to the homologies existing between these and other fungi. In a study of this group, extending over many years, I have been led to a view of the homologies between these plants and the Ascomyceteae and Basidiomyceteae, somewhat at variance with the theories of most recent writers; and it is probable that the time has come for a more definite statement of this view than has yet been given.

General Structure.

The *Uredineae* are parasitic within the tissues of higher plants, for the most part Anthophyta. They consist of septated branching threads which vegetate for some time within the host, and eventually produce spores (*conidia*) in chains, by abstriction. These spores develop upon numerous, crowded, parallel, terminal branches, within the tissues of the host, at length bursting through the epidermis. The outer conidial branches are modified into a "peridium," which surrounds the erumpent spore-mass like a tiny cup, whence the common name, "Cluster-cup," in allusion also to the fact that the spore-cups usually appear upon the leaf in clusters. For a long time these cluster-cups were supposed to have no connection with the rusts, and they accordingly were described under the generic names *Aecidium* and *Roestelia*. The first of these names is preserved in the term "aecidiospore," by which the spores are often designated. (Figs. I and II of Plate XXXII.)

Somewhat later, spores of another kind are produced singly upon the ends of other branches in the tissues of the host. These, while occurring in clusters, are by no means as closely

and regularly crowded as the aecidiospores, so that when they burst through the epidermis of the host they constitute elongated or irregular shaped spore-dots (*sori*) instead of definitely outlined cups. Here again, the spores of this kind were regarded by the earlier botanists as belonging to a distinct genus, *Uredo*: hence we commonly still speak of them as *uredospores*. They are also known as "stylospores," in allusion to the fact that they are stalked. (Figs. III and IV of Plate XXXII.)

Still later, a third kind of spore is produced, often in the uredosori, which bear some resemblance to the uredospores in being stalked, and in some cases, one-celled (*Uromyces, Melampsora*), but differing often in being two or more celled, and usually having a thicker wall. These are the last to develop upon the mycelium within the host, and when they have ripened, usually the parasite dies. Since these spores appear to complete the development of the parasite, they have long been known as teleutospores (τελευτή, "completion.") They germinate (in many species after a period of rest through the winter months) by the production of a short, several-jointed filament (the *promycelium*), from each cell of which short lateral branches develop, upon whose summits single minute spores (sporidia) are formed by abstriction. When these sporidia germinate upon the proper host they form parasitic threads which penetrate its tissues and give rise to the aecidia described above, thus completing the cycle of life. (Figs. V to XIII of Plate XXXII.)

The life history here sketched may be taken as typical, but it is subject to several modifications, e. g., (*a*) the omission of the aecidial stage; (*b*) the omission of the uredo stage; (*c*) the omission of both the aecidial and the uredo stages. Moreover, in many species the aecidial stage occurs upon a different host from that which supports the uredo and teleutospore stages, this condition being known as heteroecism, a familiar example of which may be seen in one of the common rusts of wheat (*Puccinia graminis*), where the aecidiospores develop on the leaves of the Barberry (*Berberis vulgaris*), the uredospores and teleutospores alone occurring in the leaves and stems of

the wheat. In many heteroecismal species it has hitherto been found impossible to determine the aecidium belonging to it, and for many aecidia occurring upon common plants, the uredo and teleutospore stages are not known. The difficulties surrounding this problem are so great as to discourage the attempt to solve them.

Homology of Parts.

Having now a general idea of the structure of the *Uredineae*, we come to the important question of the homology of their parts. Here, again, we are beset with difficulties. No sexual organs have yet been discovered, and there has been very much structural degeneration of the whole plant.

In their general structure the Uredineae show clearly that their relationship is with the *Ascomyceteae* or *Basidiomyceteae* rather than with the *Phycomyceteae*, and upon this point there has been little disagreement among recent botanists. Some authors regard the aecidium as a kind of degenerated apothecium, in which each conidial chain is a modified ascus. In this view, the aecidium is the result of an obsolete or obsolescent sexual act, as in the *Discomyceteae*, and the uredospores and teleutospores are considered to be conidial structures. Accordingly, those who hold this view quite consistently set off the *Uredineae* in a class bearing the name *Aecidiomycetes*. By far the greater number of botanists, however, now regard the teleutospores as basidia, homologous with the basidia of the *Hymenomyceteae* and *Gasteromyceteae*, and they therefore place the *Uredineae* in the class *Basidiomyceteae*. In this view, the sporidia which develop upon the germination of the teleutospore are basidiospores, homologous with those of mushrooms and puff balls, and the uredospores and aecidiospores are forms of conidia. It is needless in this paper to set forth these views at length, since they may be found in almost any common text-book of botany.

Briefly stated, the view which I wish to present is that the "teleutospore," so-called, is a tightly fitting ascus, containing one or more large spores; the teleutosorus is a reduced apothecium; the aecidiospores are the normal conidia; and the

uredospores secondary or accessory conidia (stylospores). In many cases the ascus-wall is readily separable from the contained spore or spores; but for the most part, the ascus-wall is so closely adherent as not to be distinguished from the spore-wall without treatment by potassic hydrate or other reagents.

In one genus, *Uropyxis*, the ascus is much larger than the double spore it contains, and may be observed very easily without special preparation. (Fig. VIII of Plate XXXII.) In *Gymnosporangium* in fresh material an ascus cavity considerably larger than the double spore can be seen in carefully made preparations. Young "teleutospores" of *Phragmidium*, in which the spores have not yet attained full size, show the ascus-wall very clearly, (Fig. IX of Plate XXXII), although in mature specimens by the enlargement of the spores it can be seen with difficulty, if at all. By careful examination, one may make out the ascus-wall in a good many cases where otherwise it might be overlooked. I have little difficulty in distinguishing it in some species of *Uromyces* (where the ascus contains but one spore) and *Puccinia* (where the ascus contains one double spore, or more accurately speaking, two spores), especially after the application of strong potassic hydrate.

The Question of Relationship.

The view here set forth, that the so-called "teleutospore" is an ascus with its contained spore or spores, involves the supposition that the *Uredineae* have suffered much structural degeneration. When we consider the fact that they are, as we may say, *intensely* parasitic, there is no improbability that we are dealing here with a greatly reduced plant structure. One has but to contrast a Dodder with a Morning Glory, or a Broom-Rape (*Aphyllon*) with a Figwort (*Scrophulariaceae*) in order to realize what great changes are produced by a parasitic habit. It has long been well known in biology that the greater the parasitism of an organism the greater is its degeneration. Some plants take but little from their hosts, and still maintain their roots, stems and leaves with so little change

that it is scarcely perceptible. It is said that some of the Gerardias are parasitic, and yet who can perceive in the countenance of any of our species any evidence of this particular vegetable sin? The closely related painted cups (*Castilleia*), however, give evidence in their appearance that their habits are not what they should be. It is even more so with *Comandra*, while the Mistletoe bears the marks of degradation upon every organ. It is not otherwise with the Carpophytes. When some ancestral seaweeds became saprophytic and parasitic, that structural degeneration of parts began which gave us the many kinds of fungi. No one may now trace with certainty the genetic line of the fungi, but that they originated from holophytic ancestors cannot be doubted; nor can there be reasonable doubt that they have become structurally more and more modified the further they have departed from holophytic habits. The holophyte requires masses of chlorophyll-bearing cells, or as we commonly express it, its vegetative organs must be well developed, but the hysterophyte has no use for such tissue, and consequently, its vegetative organs are undeveloped. The more perfectly the parasite adapts itself to its host the greater may be its departure from the structure of its vegetative organs which its holophytic ancestors developed. In like manner, the more perfectly the parasite merges itself into its host, and in a sense becomes a part of it, the more may it use the host tissues for protection and support, and the less is it necessary for it to develop protective tissues of its own. Thus we have in the fungi not only a degeneration of the vegetative tissues, but the reproductive organs have likewise undergone much degenerative modification.

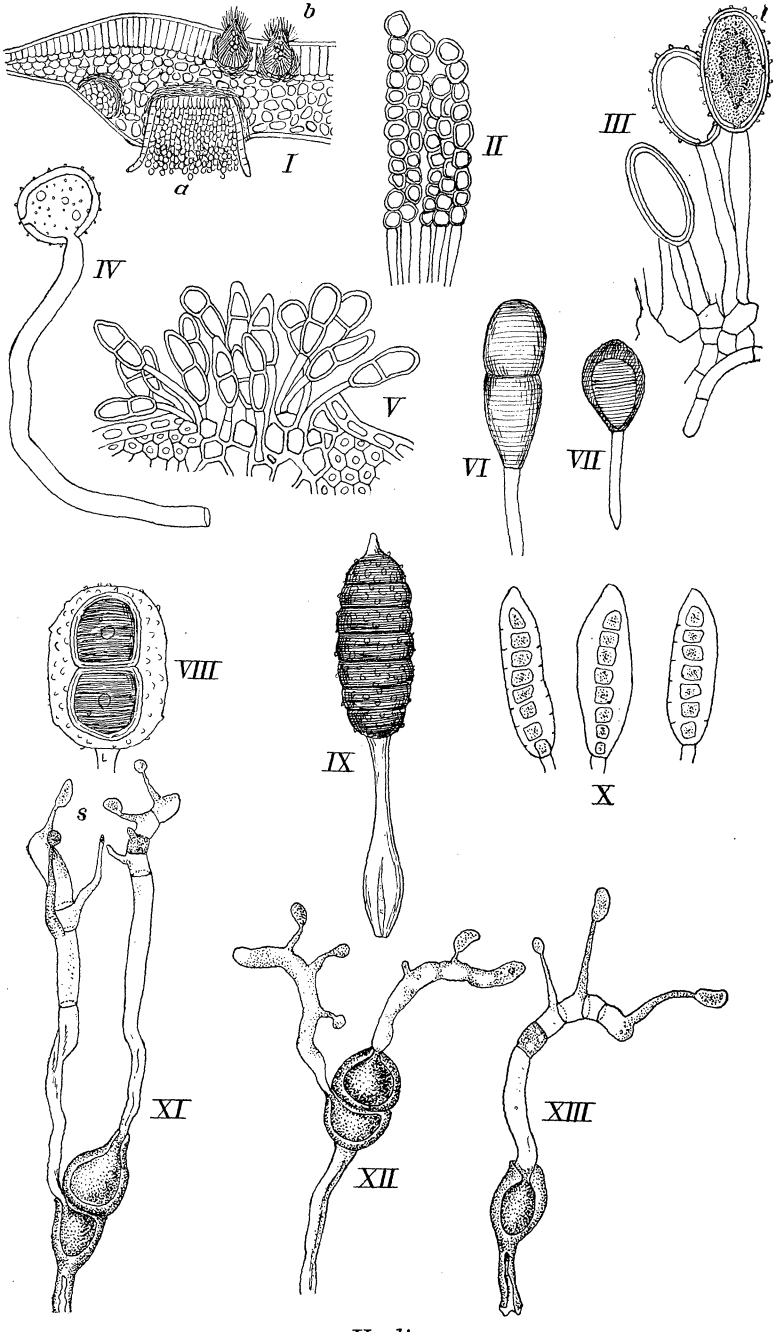
We here regard the *Uredineae* as degenerated Cup-Fungi (*Discomyceteae*), with their cups (apothecia) obsolescent, and constituting the vaguely defined teleutosori. As suggested above, there is here no need of that abundant accessory tissue which in the Cup-Fungi forms a protective envelope (exciple) around the hymenial mass, since the asci ("teleutospores") develop beneath the protecting epidermis of the host. The host-tissues in the case of the *Uredineae*, act the part of the exciple in the normal cup-fungi. The apothecia of the cup-

fungi are therefore homologous with the "sori" of the teleutospore stage of the *Uredineae.* Instead of the large eight spored asci, which are so common in the *Discomyceteae,* we find in the *Uredineae* that they are much reduced, both in size and the number of spores which they contain, there being rarely more than one or two. And here we may propose, in the light of the view here adopted, that the term "teleutospore," while a misnomer as usually applied, be retained with a restricted application to the spore or spores within the ascus. Thus we may say that the ascus of *Uromyces* contains but one teleutospore, while in *Phragmidium* it contains several. If necessary (which I doubt) to distinguish these reduced asci from normal ones, we may employ the convenient term *teleutoasci.* We may thus have *teleutosorus, teleutoascus* and *teleutospore.*

Place in the System of Plants.

It remains to say a few words as to the place in the system of plants to be assigned to the *Uredineae* in accordance with these views. From what has been said, it follows that they are to be regarded as *Ascomyceteae,* instead of *Basidiomyceteae,* as so many recent botanists assert. Further, it is held that they are degraded and much modified forms standing at or near the end of a long genetic line, and not primitive or ancestral forms from which higher and more complex ones have sprung. The cup-fungi have not been derived from the *Uredineae,* but rather we may say that, in all probability, the latter have been derived by degeneration from the former. We must, therefore, assign the *Uredineae* to a place in the *Ascomyceteae, after* the *Dicomyceteae.* All may well agree to assign the *Perisporiaceae* to the first (or lowest) place in the class on account of their slight modification from the type of the holophytic Carpophytes. From this primitive group we pass easily along three somewhat divergent genetic lines, viz.: the *Tuberoideae, Pyrenomyceteae,* and *Discomyceteae,* and from the latter have sprung the *Uredineae.* The arrangement will then be as follows:

PLATE XXXII.



Uredineæ.

CLASS ASCOMYCETEAE.

Order *Perisporiaceae,*
Order *Tuberoideae,*
Order *Pyrenomyceteae,*
Order *Discomyceteae,*
Order *Uredineae,*
Order *Ustilagineae.*

CLASS BASIDIOMYCETEAE.

Order *Gasteromyceteae,*
Order *Hymenomyceteae.*

Of the relationship of the *Uredineae* to the *Ustilagineae* I need say no more at the present time than that the latter are here regarded as still further degradations of the *Discomyceteae;* nor is this the place in which to take up a discussion of the homologies between the *Ascomyceteae* and the *Basidiomyceteae.* Upon the latter point it is sufficient to say that the ascus and the basidium are regarded as morphologically equivalent, the ascus subdiving its protoplasmic contents into spores by an internal division (forming ascospores) while the basidium accomplishes the same thing by the growth of protrusions ("sterigmata") into whose enlarged ends the protoplasm passes, after which they separate as spores (basidiospores).

EXPLANATION OF PLATE XXXII.

I. Cross section of a Barberry leaf; *a,* a cup of aecidiospores; *b,* spermogones of *Puccinia graminis,* after Luerssen × 40.

II. Rows of aecidiospores (conidia) of *P. graminis* upon their conidiophores, after De Bary × 150.

III. Uredospores of *P. graminis,* the shaded one ripe, after De Bary, × 390.

IV. Germinating uredospore of *P. straminis,* after De Bary, × 390.

V. Cross section of a teleutosorus of *P. graminis,* after De Bary, × 200.

VI. Teleutoascus of *P. graminis*, external view, after Ludwig, × 450.

VII. Teleutoascus of *Uromyces fabae*, optical section, after Ludwig, × 450.

VIII. Teleutoascus of *Uropyxis amorphæ*, optical section, after Ludwig, × 450.

IX. Teleutoascus of *Phragmidium subcorticium*, external view, after Ludwig, × 450.

X. Immature teleutoasci of *Phragmidium subcorticium*, after Bessey, × 400.

XI. Germinating teleutospores (still within the ascus) of *Puccinia graminis*; *s.* sporidia, after Tulasne, × 400.

XII. Germinating teleutospores (still within the ascus) of *Puccinia moliniae*, after Tulasne, × 400.

XIII. Germinating teleutospore (within its ascus) of *Uromyces appendiculatus*, after Tulasne, × 400.